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REPRODUCTION BY LAYERING AMONG CONIFERS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 149

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(WITH ONE FIGURE)

Many types of plants multiply more or less by layering, or may be made to do so by artificial means. The fact seems not to be well known that various conifers, particularly members of the genera *Picea* and *Abies*, possess this power and multiply by it to some extent. Having by accident discovered a case of layering in the balsam fir (*Abies balsamea* [L.] Mill.) during the course of ecological work on Isle Royale, Lake Superior, I found that the habit was a factor of considerable importance in the dynamics of the forest. Investigation into the literature of the subject brought to light a few scattered references to layering of coniferous trees, which are noted below. It is not probable that the list is exhaustive.

I. Literature

The earliest description that was found was contained in LOUDON'S *Arboretum et Fruticetum Britannicum* (**8**), vol. IV, pp. 2297–2298. The author quotes Mr. JAMES M'NAB in *The Gardener's Magazine* as follows:

> From the pendent habit of the lower branches of the spruce (*Picea excelsa* Link) some curious anomalies are occasionally found in its habit of growth. The shoots next the ground, when they have attained a considerable length, naturally rest on the soil at their extremities; and the soil being kept moist by the shade of the branches, these often root into it; and the points of their shoots taking a vertical direction, a series of new trees are formed in a circle round the old tree.

A particular specimen, growing in Scotland, is described thus:

> Many natural layers from the trunk and from the primary substems have taken root, so as to form a double series of young trees in two concentric circles round the parent trunk.

A little farther on is the following:

> That portion of the branch which is between the trunk of the original tree and the part where it roots into the ground, and which is sometimes several feet in length, rarely increases in diameter after its extremity has rooted. . . . .

> The branches proceeding from the primary substems have also branches, equally healthy with themselves, proceeding from them, and with every appearance of their producing others. . . . . The primary substems, which constitute the inner concentric circle of young trees, vary from 8 feet to 25 feet in height; and the secondary substems, which form the trees of the outer circle, are from 4 feet to 10 feet high. There are upward of thirty rooted stems surrounding the mother tree, and 30 feet is the greatest diameter of the space covered by stoloniferous branches; though in one case a secondary layer has reached as far as 18 feet from the main trunk.

LOUDON also mentions cases of abundant layering in *Abies nigra* (*Picea mariana* [Mill.] BSP.).

KUNZE (7) also refers to M'NAB'S observations and concludes from these and other cases that "Coniferae, especially the Abietineae, possess widely extended power of root formation and are able to send out rooting shoots."

KIHLMAN (6) notes that *Picea excelsa* growing at the arctic tree line in Lapland spreads extensively by layering. He describes the occurrence of the habit as follows. The lowest branches often have roots, and from their tips new erect shoots develop, which become treelike in form and come to lead independent lives; from this results a complex of shoots and small trees of various ages, which is very sharply bounded, and which often arises from a single parent. Such a group, 4 meters in diameter, included 42 stems more than 4 cm. thick, besides numerous smaller ones. The age of such a centrifugally spreading group of spruces may almost be unlimited. He distinguishes two habit varieties of *Picea excelsa*. One possesses a tall cylindrical crown, often extending to the ground, the lower branches seldom rooting, and the life of the individual thus ending with the death of the main trunk. The other variety, characteristic of the region of the northern limit of the spruce, is low and scrubby, and layers abundantly as described above.

CHRIST (2) refers to layering in *Picea excelsa* as of rare occurrence, and names such forms *Picea excelsa forma stolonifera.*

GOEBEL (5) mentions cases of layering in *Picea excelsa*, *P. nigra*, and *Abies sibirica.*

SCHRÖTER (11) describes and illustrates something very similar in the case of *Pinus montana* in the timberline belt of the Alps.

He speaks of "horizontal snakelike branches crawling over the ground, ascending or erect at the ends," but does not state, nor do his figures show, that these branches take root.

According to MAYR (9) all deciduous trees and conifers are able to produce roots when branches or weak stems are bent down and placed in contact with the ground for a time. He mentions the following genera as among those that have been observed to reproduce by layering: *Abies*, *Picea*, *Pinus*, *Larix*, *Pseudotsuga*, *Chamaecyparis*, *Cryptomeria*.

MIGULA (10) briefly notes the habit, and gives an illustration of a spruce (*Picea excelsa*) surrounded by a circle of young trees developed from layered branches.

VOGTHERR (13) speaks of the habit as occurring frequently, though often overlooked, and states that it is commonest in moist habitats in northern latitudes and in mountain regions.

Reproduction by layering among conifers has been reported in America, so far as I have been able to discover, in two species only, both of the genus *Abies*.

SUDWORTH (12) in discussing the reproduction of the alpine fir (*Abies lasiocarpa* [Hook.] Nuttall) says (p. 111): "Occasionally at high elevations branches lying on ground take root (layer), from which, however, reproduction is probably rare."

In *Silvical Leaflet* (4) of the Forest Service, devoted to *Abies lasiocarpa*, is the following paragraph:

> Alpine fir frequently exhibits a tendency to reproduce by layering. The lower branches, which are procumbent, become covered with earth, roots are produced, and the branches increase in size and assume an upward curve. It is doubtful, however, if the tree ever actually reproduces itself in this manner. The tendency becomes more apparent with increasing altitude, the main trunk becoming shorter, while the layered branches form a saucer-like whorl at its base.

CLEMENTS (3), speaking of the same species in the Colorado mountains, states that "all the young firs examined had started by layering from the lower branches of parent trees."

Concerning the eastern balsam fir (*Abies balsamea* [L.] Mill.) I have found but one notice of the habit. CHITTENDEN (1) in discussing the timberline trees of the White Mountains says:

Balsam, at such elevations, rarely matures its seed, reproduction being dependent on seed blown up from below and on the layering of the trees themselves. Branches so layered are often found growing as independent trees, the connecting branch having decayed. The rooting always proceeds from dormant buds. Prostrate balsam occurs at an altitude of 5500 feet on the Presidential Range, where it reproduces almost entirely by layering. At an elevation of 4900 feet cones are borne sparingly, but even here reproduction by layering exists.

II. Layering as observed on Isle Royale, Lake Superior

Upon Isle Royale the layering habit manifests itself as follows. In the forest one frequently comes upon small groups of young balsams, often of about half a dozen individuals of various sizes. These upon superficial inspection would easily pass for a cluster of seedlings, but if the group be carefully dug up, all the young trees will be found to be connected with each other a little below the surface of the ground. The way in which the layering comes about was found to be as follows. The lower branches of the balsam droop more or less, and the middle portion of such a branch frequently becomes covered with moss, litter, and humus. If the point of origin of the branch is very close to the ground, the connection soon becomes entirely concealed; this seems to be the case more often than otherwise. The covered portion now produces roots abundantly, and the tip becomes erect, loses its dorsiventral character, takes on radial symmetry, and is to all appearances a perfect miniature tree.

Layering may take place at any stage in the life of the tree. Sometimes the layered branch may be only a few years younger than the parent and not very perceptibly smaller, showing that it must have developed from one of the very earliest branches. Mere seedlings were sometimes seen with layered branches about as large as the parent. The daughter trees often produce a second generation, and it is in this way that the groups of apparently independent saplings come into existence. On the other hand, cases were found where a mature tree was layering through branches that had their points of origin a number of decimeters above the ground. Several of the lower branches of a mature tree may layer, producing a circle of young trees around the parent, and numerous cases were found in which the layered branches themselves had given rise to secondary groups, the connection with the original tree being still maintained.

There is abundant evidence that in many cases the layered branches become independent trees by the decay of the connecting portions. In fig. 1 it may be seen that the layered branch near its point of origin is extremely slender, while in the region where the roots have developed and in the subaerial portion it is thick. The transition from thin to thick is frequently very abrupt. This points toward the conclusion that the young tree is deriving by far the greater amount of its sustenance from its own root system, and that if the connection should be broken it would be entirely able to care for itself. The underground portion was often so weak that in spite of the greatest care it was severed in the process of uprooting. In many cases also the decumbent bases of independent young balsams indicate that they once had a horizontal connection with some neighboring tree (see *a* in fig. 1).

Some examples will make clear the various forms which the habit of layering takes.

1. A very typical case is seen in fig. 1. The oldest stem shown in the photograph is at *1* (all but the base has been removed for the sake of clearness). That this is itself a layered branch of a still older tree is indicated by the long rhizome-like structure (*a*) extending horizontally toward the left. The character of the well formed young tree *2* as a layered branch of *1* is evident. Branch *2* is one meter high. Branch *3* is connected with *2* by way of *c*, and has itself given rise to *4;* the latter finally has produced *5*. There are thus represented five generations of upright stems produced by repeated branching and layering. Each except the youngest possesses a well developed root system of its own, and in every case except the last the horizontal connecting stem behind the region of vigorous rooting has remained practically without further development. The constriction where *b* joins *1* is especially evident. Branch *5* receives all its nourishment from *4*, and the latter probably still derives much from *3*.

2. A balsam 2 meters high, which had died very recently at the age of 46 years, itself apparently a layered branch, had given rise

through a lower branch to a young tree 7.5 dm. high, 24 years old, 2.5 dm. distant from the parent. This daughter tree was found to have produced four smaller ones, 1.5–6 dm. in height, with ages ranging from 16 to 22 years.

3. That the habit may show itself even in large and mature individuals is proved by the following case. This tree, a balsam 1.5 dm. in diameter and 85 years old, had given rise to a daughter tree through a layered branch which started 7.5 dm. above the ground. The outer portion of this branch was soil covered and had well developed roots. At a distance of one meter from the parent it became a symmetrical tree 1.3 m. high. The same large branch had also produced two smaller trees by the layering of secondary branches.

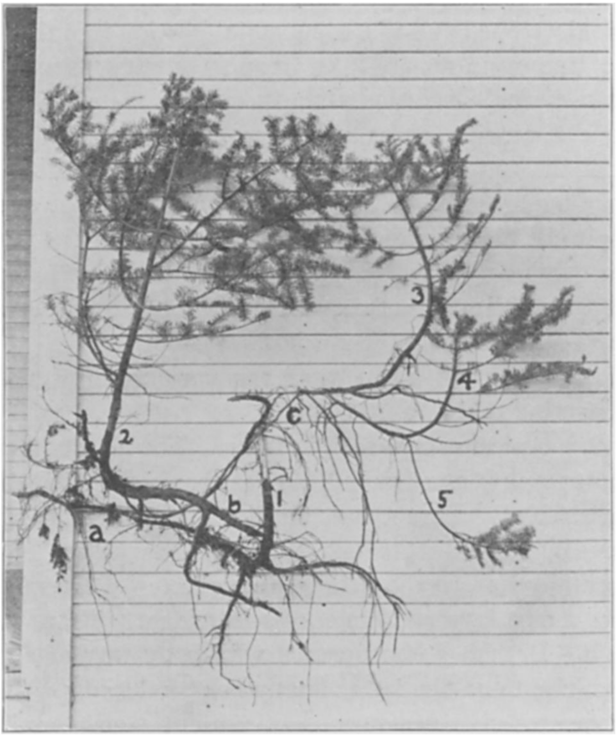

FIG. 1.—An example of layering as it commonly occurs on Isle Royale, Lake Superior; *Abies balsamea.*

4. A balsam growing in a large rock crevice at the forest edge on an exposed shore had several layered branches, erect at tip, through the soil at the general level of the ground. Several similar branches, at about the same elevation but in line with the crevice, descended into it somewhat, but their ends were erect, radially symmetrical, and perfectly treelike. Since the crevice was a foot wide and contained no soil, no roots were formed in this case, and these branches remained entirely dependent upon the tree.

Aside from the balsam, layering was less frequently observed in every one of the coniferous trees that occur upon Isle Royale. It was fairly common in the case of the black spruce, perhaps being favored by the pronounced droop of the lower branches of that species. The black spruce occurs sparingly in the upland forest, and in this habitat the layered branches were identical in behavior with those of the balsam. Black spruces and tamaracks growing in bogs were found to layer abundantly through the rapidly growing sphagnum. Specimens of white spruce were found upon nearly bare rocks, whose lowest branches, covered with a thin mantle of humus, had developed the layering habit to such an extent that the parent had become entirely surrounded by a group of daughter trees. Similar groups were seen in the case of arbor vitae growing in a river swamp.

III. Conclusions from data presented

From the material here presented we gather that the habit of natural layering among coniferous trees is common and widely distributed, though its importance appears to have been generally overlooked, at least in this country; that it is particularly characteristic of the closely related genera *Picea* and *Abies*, but is found in many other genera, among which are *Larix*, *Thuja*, *Pinus*, *Pseudotsuga*, *Chamaecyparis*, and *Cryptomeria;* that it is most prominent in northern and mountain regions, and that it occurs more frequently and attains more striking development with increasing latitude and altitude; that its best development is found at the extreme limit of the forest—the arctic tree line and the mountain timberline.

The general region of its occurrence is practically that of conifer dominance; its increased development in high latitudes and altitudes is not so easily explained. VOGTHERR (**13**) correlates the layering tendency with a moist habitat, made possible by the low evaporation rate in northern and mountain forests, and it is doubtless true that moisture and absence of light are the factors that stimulate the buried portions of the branch to root production. But cases were noted (see example 4 above, and also SCHRÖTER **11**), in which, although the end of the branch became erect and treelike, no portion was buried, and therefore no roots were formed. In other cases trees with layered branches were found growing in xerophytic situations upon the exposed rocky shores of Lake Superior. Timberline conditions, too, more often than not, are xerophytic in the extreme. The connection with a moist habitat thus seems not to be an essential one. In explanation of the striking cases of layering reported from the tree line in various regions (circles and double circles of daughter trees surrounding the parent), it may be noted that in such localities the forest is open, and the trees therefore, on account of abundance of light, are clothed with living branches to the ground. Moreover, they are as a rule short, bushy, and branchy, and the low crown tends to spread horizontally rather than to increase in height. Just such conditions as are found here (numerous healthy branches close to the ground) are those which would apparently most favor the appearance of the layering habit. In the endeavor to solve the problem, however, the meagerness of the data should be borne in mind. It may be that more extended and careful observation would prove that the habit is as common at low latitudes and altitudes as at high. Possibly the greater number of reports from arctic and alpine regions is due to the fact that the phenomenon is most easily observed there, or that individual cases of more striking appearance have been found. On Isle Royale, though the habit was exceedingly common, no such remarkable examples were discovered as those reported by LOUDON and KIHLMAN.

IV. Ecological importance of layering

The habit of layering, in regions where it occurs, must be included as an important factor in any investigation of forest dynamics. For example, in the climax forest of Isle Royale there is an appearance of thick reproduction, with a great preponderance of balsam in the young growth. Upon superficial examination one would conclude that reproduction by seed is taking place at a tremendous rate. Careful investigation reveals that a large proportion of the apparent seedlings are in reality merely layered branches, some of them having originated from mature trees, and many others being groups of connected shoots which have started from a single true seedling. The same situation was found by CLEMENTS (3) in Colorado. It is evident that the effectiveness of this method of reproduction will have an important bearing upon the course of the succession in the forest. The habit is of special importance in the region of timberline, where, according to authors quoted above, it is sometimes almost the only method of reproduction.

V. Physiological bearing

There are also physiological problems involved in the phenomena of layering in this group of plants, which cannot at present be satisfactorily settled. These problems relate to the theories of orthotropism and plagiotropism and their mutual relations. The whole subject is at the theoretical stage, without adequate evidence in support of any of the various hypotheses. In the process of layering, the rooting (when it occurs) is simple enough as a response to moisture and absence of light. The change from dorsiventral to radial symmetry is to be expected as a result of the tip becoming erect, being an adjustment to changed light relations. The change in direction of growth from horizontal to erect is the part that is difficult to explain. It is bound up with the agencies which cause lateral shoots, ordinarily plagiotropic, to become orthotropic when the terminal shoot is removed or damaged. In the process of layering, it should be noted, this change takes place without antecedent removal of the main shoot. The case is thus somewhat different, but the same factors doubtless govern it. In the present state of knowledge relating to orthotropism, plagiotropism, and correlation, it will be useless to continue the discussion at length. One point however seems to be important enough in its bearing upon the physiological side of the question to justify a few words in conclusion. GOEBEL (**5**, chapter iii), to explain the replacement of the terminal by a lateral shoot, offers the theory that the change in direction of growth of the lateral comes about because of changed conditions of nourishment. He thinks that the main transpiration current, which ordinarily goes to the terminal shoot where growth is most vigorous, is deflected when the terminal shoot is removed, and passes into the uppermost lateral. The great increase in nutrition acts as a stimulus, causing the lateral shoot to become erect. He describes several cases of layering among conifers, and attributes the change in direction of growth of the layered branch to the same factor. In this case the increased amount of food materials which acts as the stimulus is furnished through the agency of the newly formed root system. This theory would fit most of the cases of layering which have been described, but in one example which came under my observation on Isle Royale (no. 4 above) the change of direction of growth took place with absolutely no root formation. The same is probably true of those described by SCHRÖTER (**11**). Here are cases, therefore, where GOEBEL'S explanation certainly does not hold, and so far as this bit of evidence goes, it throws doubt upon his theory as a whole.

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